

Identifying reference communities in ecological restoration: the use of environmental conditions driving vegetation composition

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- 1 Identifying reference communities in ecological restoration: the use of environmental
- 2 conditions driving vegetation composition
- 3 **Running head:** Identification of references in ecological restoration
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- personalized R functions; AD, RJ, AB analyzed results; AD wrote the first draft; AD, AB, RJ,
- 19 EB revised and edited the manuscript.

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Abstract

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In restoration ecology, the reference ecosystem represents a key concept which is well defined from a theoretical point of view. In practice, however, selecting reference systems, such as reference plant communities, often lacks clear methodology. In order to facilitate this selection, we provide a framework based on ecological theory and more precisely on relationships between vegetation and environmental factors to identify reference plant communities. The four major steps are: 1) the delimitation of a geographical zone in which habitat types similar to restoration sites occur; 2) the identification of environmental factors structuring non-degraded plant communities within this geographical zone; 3) the comparison of the environmental factors between non-degraded and degraded sites; 4) the selection of the non-degraded sites most similar to restoration sites in terms of environmental factors to use them as references. We concept-proved our approach by identifying reference communities using environmental factor combinations for five mountain grassland sites degraded by the construction of a high-voltage line. In a multivariate analysis of eighteen non-degraded sites, we identified six major environmental factors explaining plant species compositions. A second multivariate analysis including degraded sites provided environmental distances of the eighteen non-degraded to each of the degraded sites. The results demonstrated that the environmentally most similar sites were not necessarily the geographically closest ones. In conclusion, the analysis of regional plant-environment interactions provides an important tool to identify reference communities or source sites for seed transfer if not available adjacent to degraded habitats.

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- Keywords: abiotic factors, grassland restoration, plant succession, degradation, target
- 45 reference

Implications for Practice

- A good knowledge of the relationships between structuring environmental factors and plant community composition allows the identification of reference communities based on the measurement of these factors at restoration sites. - The selected environmental factors need to be robust and should not be too much affected by ecosystem degradation prior to restoration. - The study of several potential reference communities makes it possible to select the best reference(s) for each restoration site in terms of such environmental factors. - In grassland ecological restoration, the identification of reference communities using combinations of factors of restoration sites allows a more efficient sourcing of donor sites in particular if close-by reference communities are not available.

Introduction

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The definition of reference systems is a crucial step in ecological restoration as it allows defining restoration targets and evaluating restoration success (Hobbs & Norton 1996; Giardina et al. 2007; McDonald et al. 2016). The reference paradigm represents a cornerstone concept which is well defined from a theoretical point of view (Aronson et al. 1993, 2016; SER Primer 2004). However, in practice, the specific selection of reference ecosystems or communities often lacks clear scientific criteria, or this step is not sufficiently taken into account in restoration planning. A review of 301 articles focusing on terrestrial ecological restoration projects showed that less than 75% of the studies used a reference, 62% used "negative reference(s)" representing the pre-restoration degraded state, and only 60% used "positive target reference(s)" defined by the pre-degradation system, with only 22% presenting both. Both negative and positive references may be used together to evaluate restoration success: i) a negative one to evaluate the success of an active restoration compared with the degraded system , and ii) a positive one to assess success by comparing the restored and the reference communities (Benayas et al. 2009; Wortley et al. 2013). In many studies, the ecosystem prior to its degradation is considered as a (positive) reference (Aronson et al. 1995; SER Primer 2004). However, ecosystems may already be degraded prior to the latest disturbance that is considered as starting point of restoration, and/or the information on the state of the ecosystem before degradation might not be available. This is a very common situation in European grassland restoration where ecosystems suffer from land abandonment or intensification (Bischoff 2002; Baasch et al. 2016). An important objective of restoration is to accelerate or jumpstart succession by facilitating late-successional species (Palmer et al. 1997). Late-successional stages or even endpoints of succession are determined by abiotic conditions although historical contingency may influence final community composition (Fukami et al. 2005; Young et al. 2005). While it is useful to

consider endpoints (attractors) of succession, earlier successional stages and potential variation of endpoints also need to be taken into account (Prach et al. 2016). The succession towards natural vegetation representing such endpoints is often prevented by human land management. A constant and/or predictable disturbance regime, such as grazing by livestock of semi-natural grasslands, may result in stable intermediate states of plant succession (or "alternate steady states" or metastable states; Clewell & Aronson 2013). These intermediate states can thus be considered as quasi-stable representing an equilibrium with environmental conditions and land management (Young et al. 2001; Bouzillé 2007). The use of several positive references may be a solution to take into account such intermediate states and is increasingly common in ecological restoration (Ruiz-Jaen & Aide 2005; Suganuma & Durigan 2015; McDonald et al. 2016). The definition of various reference systems resulting from different land management types (Le Floc'h & Aronson 1995; Cortina et al. 2006) would provide a range of restored ecosystem trajectories. Furthermore, considering the potential variation in successional endpoints allows integrating ecosystem dynamics and natural variability (Asbjornsen et al. 2005; Sluis et al. 2018; Erskine et al. 2019). In cases of high spatial heterogeneity such as varying slope and aspect, small-scale differences may compromise the preference of adjacent plant communities and populations usually recommended for active ecological restoration (Kiehl et al. 2010, Vander Mijnsbrugge et al 2010; Scotton et al. 2011). Additionally, restoration sites may sometimes be surrounded by other more or less degraded ecosystems. In such cases, references need to be found at higher distances requiring a clear concept and methodology to identify the most appropriate sites. In our study, we provide a framework to define positive reference communities by using environmental factors that drive plant species composition. This method is particularly useful in the following cases: i) information on plant species composition prior to latest degradation is not available; ii) the sites were already (at least partially) degraded before the latest

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disturbance for which restoration is required and several environmental factors structuring plant communities remain within the natural range after a particular ecosystem degradation; iii) if due to economic or legal constraints, only one propagule source site can be selected for several restoration sites.

We first present a framework to select reference communities by using environmental factors that determine plant species composition. To concept-prove our framework, we applied the approach to a mountain grassland project involving the restoration of temporary access tracks required to build a new high-voltage electricity line. Habitat conditions at the sites change at relatively small scales thus complicating the search for appropriate reference communities. Such extensively grazed and/or mowed grassland ecosystems represent a particular case of succession in which regular management truncates succession by preventing the development of woody vegetation (Young et al. 2001). Most European grasslands are thus considered as such alternative quasi-stable states since they are maintained by regular grazing and mowing. Their species composition is not only dependent on climate and soil conditions but also on management type (Isselstein et al. 2005; Härdtle et al. 2006). However, management regimes are similar in our study region allowing an analysis of environmental factors driving plant community composition. Due to the scope of the construction work, the different non-degraded grasslands selected as potential references should thus make it possible to obtain a wide range of quasi-stable states representative of the different restoration sites.

Framework to identify reference communities by combinations of environmental factors

We suggest a 4-step methodological framework to select references by analyzing the species composition of non-degraded systems and measuring the environmental factors structuring them (Fig. 1): 1) delimit a geographical zone in which habitat types similar to restoration sites occur; 2) identify environmental factors structuring non-degraded plant communities within this geographical zone and measure them in non-degraded and degraded sites; 3) evaluate environmental distances between degraded sites and non-degraded sites; 4) identify the nondegraded sites most similar to restoration sites in terms of environmental factors. First, a rough estimation of habitat type based on existing habitat or biogeographical maps is required to delimit the geographical zone in which the reference communities may be found (Alard 2002). Existing pedoclimatic or historical vegetation data may increase the precision of habitat type information. Secondly, within the delimited geographical zone, major environmental factors that typically drive species composition in the study area are measured on non-degraded sites. Factors that are significantly modified by the habitat degradation cannot be taken into account. At the same time, the relationship between these environmental factors and plant species composition is analyzed. The number of analyzed sites needs to be representative of the variation of the geographical zone and sufficient to identify the best subset of environmental factors using multivariate statistics. Once identified, the major environmental drivers of nondegraded sites need to be measured on sites to be restored. The non-degraded sites presenting the most similar values compared with restoration sites can therefore be used as reference sites. This method allows identifying the best corresponding plant communities for each restoration site within the study zone. For each restoration site, one or more reference sites that correspond best in terms of structuring environmental factors and thus of potential plant community composition will be chosen.

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Proof of concept

We tested our approach to identify reference communities using combinations of environmental factors in mountain grasslands degraded by the construction of a high-voltage electricity line. The construction work included the creation of access tracks and working platforms on 13 ha of mountain grasslands. The grasslands were separated in hundreds of patches separated by woodlands. Due to small-scale changes in abiotic conditions and degradation of adjacent sites by land abandonment, arable use or afforestation, the closest sites were often inappropriate references. The identification of reference communities was thus a priority action to define restoration targets but also to find appropriate grassland sources for hay transfer used as a restoration technique (Kiehl et al. 2010). Following the four suggested steps we asked: (1) What are the environmental factors explaining best the species composition of non-degraded mountain grassland sites? (2) What are the non-degraded sites most similar to the degraded sites in terms of these environmental factor combinations? (3) Are the environmentally most similar sites also the geographically closest ones?

Material and methods

Restoration sites and delimitation of geographical zone

The study area is the upper Durance valley ("Haute-Durance") in the Southern French Alps from L'Argentière-la-Bessée to La-Batie-Neuve (44°78'78''N, 6°59''41'E; 44°57'93''N, 6°20''77'E, Fig.2). The study sites are located 100 to 600 m above the valley floor on slopes at an elevation of 1000 to 1400 m (upper montane altitudinal belt). The climate is temperate to sub-Mediterranean depending on elevation and exposition. The Pelvoux and Mont Viso mountains provide a rain shadow, reducing precipitation to 740 mm per year, with a mean annual temperature of 10.7°C (based on data from 1991 to 2010, meteorological station of Embrun). The bedrock is predominantly calcareous, but many sites are covered by quaternary

glacial deposits. The degraded areas were characterized by dry to mesophilic grasslands. Most of these grasslands are Natura 2000 priority habitats: "Semi-natural dry grasslands of *Festuco-Brometalia* and scrubland facies on calcareous substrates" (N6210, EU directive habitat 92/43/EEC). The construction work affected soil structure and soil organic matter composition by stripping soil, compacting and decompacting. A total of 18 species-rich non-degraded grassland sites as well as five restoration sites were selected as study sites in the Haute-Durance valley (Fig. 2). Selection criteria were traditional management by grazing (sheep, cattle) and mowing, geographical representation of the study area and representative microclimatic conditions (semi-dry to mesophilic) in avoiding driest and most humid sites. We further excluded restoration sites with particularly strong soil modification by gravel addition.

Data collection

To link species composition to environmental conditions, vegetation cover of all vascular plant species was evaluated between 21 June and 5 July 2018 in 3 randomly placed quadrats (2m x 2m) within each of the 18 non-degraded grassland sites resulting in a total of 54 quadrats. We measured abiotic factors that are usually not or little influenced by soil disturbance involved in access track or working platform creation. These factors included soil variables such as phosphorus, potassium and carbonate content, pH value and moisture but also geomorphological variables influencing climatic conditions such as slope, aspect and elevation. Three soil samples per site were thus taken to a depth of 20 cm (diameter 5 cm). They were dried and sieved using a 2 mm mesh size. Plant available phosphorus (P₂O₅) was determined using the Olsen Sterling method (1954), exchangeable potassium ions (K₂O) was determined according to Thomas (1982) and Ciesielski et al. (1997). Soil moisture was measured in the field using Theta Probe ML3 sensors. The soil pH was measured in a 1:5 water solution. The carbonate content was estimated using a 3-level scale of effervescence with 1 M HCl (non-

effervescent; slightly effervescent; strongly effervescent). In mountain ecosystems, plant species composition and richness are strongly influenced by slope and aspect driving solar radiation (Pykälä et al. 2005). We estimated the annual direct incident solar radiation (ASR) using the method of McCune & Keon (2002). The ASR takes into account that southwest facing slopes show a higher radiation than southeast-facing slopes in folding the aspect (Supplement S1). This folded aspect is combined with slope and latitude to calculate the ASR.

Statistical analysis

Factor selection: test of variance inflation to avoid collinearity and correlation matrix

In order to reduce collinearity within the measured environmental variables we tested Variance

Inflation Factors (VIF; Zuur et al. 2010). Highly correlated variables (VIF>2) were sequentially

removed (R package "vegan", Oksanen et al. 2019). We used the pairwise correlation analysis

(Pearson correlation coefficient) to crosscheck VIF removal procedure. Since slope and aspect

are included in the ASR, they were not considered. Carbonate content (correlated to pH) was

removed according to VIF analysis whereas elevation, ASR, soil moisture, soil pH, P₂O₅ and

K₂O were kept and used in subsequent analyses in order to test the response of plant species

composition to environmental factors of non-degraded sites.

Analysis of factors driving species composition

(RDA) to model the relationship between species composition and environmental variables (R package "vegan", Oksanen et al. 2019). Species cover was first Hellinger-transformed since this transformation provides a better resolution in linear ordination techniques than chi-square distance (Legendre & Gallagher 2001). We removed rare species (occurring in less than eight

We analyzed the plant species composition of the non-degraded sites using redundancy analysis

plots) from the analysis in order to improve the detection of relationships between community

composition and abiotic factors. Removing rare species reduces bias due to stochastic sampling

effects since rare species occurrence is often a poor predictor of environmental conditions (McCune and Grace 2002). The significance of the six selected variables (ASR, elevation, soil moisture, soil pH, P_2O_5 , K_2O) was tested using the "envfit" function with N = 999 permutations (R package "vegan"; Oksanen et al. 2019) to determine relationships with plant community composition.

Environmental distances between non-degraded and restoration sites

The environmental distance (= dissimilarity) between each restoration and non-degraded sites was assessed by calculating the Euclidean distance using the "vegdist" function (R package "vegan"; Oksanen et al. 2019). Non-metric multidimensional scaling (NMDS) based on Euclidean distances of environmental factors was used to illustrate the most similar reference for each restoration site (R code: https://github.com/RenaudJau/ChooseRef). In order to compare the distribution of plant communities according to environmental factors values and to geographical zone, a second NMDS was performed on plant species composition of non-degraded sites. Sites were grouped by each environmental factor (high, medium, low factor values) and major geographical zones (south; central; north) in different ordination plots. All analyses were performed using R 3.5.3 (R Core Team 2019).

Results

Environmental drivers of plant species composition

One-hundred and eighty plant species belonging to 40 families were identified across the 18 study grasslands. The RDA model relating plant species composition and environmental variables at non-degraded sites explained 44.8% of the total variance. The first two constrained axes accounted for 20.2% and 11.4% of total variance and were mainly determined by P_2O_5 , soil pH, soil moisture and solar radiation (Fig. 3). The environmental variables retained by the VIF analysis did not show strong correlations confirming that applying it efficiently removed correlated environmental variables (Table S1). Four of the six selected variables (ASR: p =

0.004, P_2O_5 : p = 0.025, soil moisture: p = 0.023, pH: p = 0.026) had a significant influence on plant species composition whereas the influence of elevation (p = 0.201) and K_2O (p = 0.830) was not significant (Table S2). Sites located on the right side of Fig. 3 were associated with low ASR, relatively low (neutral) pH and high soil moisture, as well as high P_2O_5 . They were well represented by mesophilic species, such as *Dactylis glomerata*, *Galium verum*, *Poa pratensis*, *Plantago lanceolata* and *Lathyrus pratensis*. In contrast, plants associated with higher ASR and pH included *Bromopsis erecta*, *Brachypodium rupestre*, *Pilosella officinarum*, *Lotus corniculatus* and *Teucrium chamaedrys*. Sites with higher abundance of *Astragalus danicus*, *Pillosella officinarum*, *Lotus corniculatus* and *Teucrium chamaedrys* were negatively correlated with elevation and soil moisture, whereas sites with higher abundance of *Salvia pratensis* and *Dactylis glomerata* were positively correlated with both environmental variables.

Identification of reference sites by comparing similarity in environmental factors

The five restoration sites revealed different combinations of environmental factors resulting in different environmental distances with non-degraded sites (Fig. 4). Restoration sites 1R and 3R showed a low environmental distance to the non-degraded site 21 indicating high similarity in measured abiotic factors. However, the second environmentally closest non-degraded sites were different (1R: site 22, 3R: site 18). The three sites closest to 2R in terms of environmental variables were 6, followed by 4 and 5. The most similar sites to 11R were 12, 10 and 16, and the most similar to 20R were 9, 17 and 14 (Fig. 4.a, Table 1). If technical and/or logistic constraints require the choice of one reference community as a source site for plant material for all five degraded sites, the non-degraded site 9 would represent the best reference (Table 1), which has the lowest mean distance to five restored sites (Fig. 4.b).

The geographical zonation of plant species composition hardly corresponded to environmental factor values. NMDS according to geographical position separated the southernmost zone from the northernmost zone whereas the central zone was not well separated from the latter one (Fig. S1). The Northern zone was characterized by low levels of P₂O₅ and soil moisture, low solar radiation (ASR) and neutral pH. The Central zone showed highest soil moisture and P₂O₅, medium ASR and the most acidic pH. The Southern zone was represented by high solar radiation and a basic pH. However, there were many exceptions to these general trends and environmental zonation was very different from geographical zonation in P₂O₅ and soil moisture. The lack of correspondence between geographical and environmental zonation explains that the environmentally most similar non-degraded site was not necessarily the geographically closest one.

Discussion

Our results indicate that among the seven tested environmental factors, ASR, soil moisture, P_2O_5 and soil pH best explain the distribution of plant communities in our 18 species-rich mountain grasslands and can thus be used as indicators for reference communities in this particular case.

The simultaneous analysis of environmental factors such as pedoclimatic variables, and vegetation, allows identifying major ecological processes that govern the studied system, since they are considered as major drivers of plant community composition (Box 1981). Elevation known has an important driver of mountain grassland composition did not significantly influence plant species compositionsince limited to a relatively small elevational gradient of 400 m. ASR included slope and aspect that are known to determine plant species composition in mountain grasslands (Srinivasan et al. 2005). As many other plant communities, grasslands are controlled by edaphic factors, such as water content, organic matter and nutrient

concentration (Sebastiá 2004; Klimek et al. 2007). Several studies have emphasized the relation between pH and phosphorus. Phosphorus availability decreases with increase in pH because at alkaline pH, phosphate ions react with calcium or magnesium (Cerozi & Fitzsimmons 2016; Li et al. 2019). This is consistent with our results that show a negative correlation between soil pH and exchangeable phosphorus (P₂O₅).

restoration ecology (Halle & Fattorini 2004) although some recent studies have developed a more explicit methodology. Suganuma & Durigan (2015) selected nine references divided into three categories of riparian forest according to their ecological integrity (3 references in old growth forest, 3 in degraded forest and 3 in secondary forest). Erskine et al. (2019) combined vegetation surveys and mapping data to select five reference sites for the ecological restoration of uranium mines, while McManamay et al. (2018) suggest a spatial framework in six steps to identify reference systems for stream restoration. All these studies used multiple references that were selected according to relationships between environmental factors and vegetation patterns. They included floristic surveys (contemporary data) and the search of historical data. These studies suggest extending the surveys beyond the close vicinity of restoration sites and using statistical tools to identify and to rank structuring variables in order to select appropriate reference communities. In our framework, we filled this gap in providing a method to identify reference plant communities based on statistical analyses of specific relationships between environmental factors and plant community composition.

Since soil conditions are among the most important factors driving plant species composition, a careful variable choice is needed to exclude factors strongly influenced by previous ecosystem degradation. Soil disturbance, such as tillage or soil removal, may lead to a drastic reduction in organic matter and total nitrogen storage, and can strongly affect their distribution in the soil profile (Hölzel & Otte 2003; Dolan et al. 2006; Du et al. 2010). Intermediate arable use, as the

plant available potassium and phosphorous (Bischoff et al. 2009). In such a case of eutrophication, the depletion of fertilizer residues is crucial to obtain abiotic conditions that are appropriate for the establishment of plant species adapted to the pre-degradation state (Tallowin et al. 1998; Bischoff et al. 2009). Thus, our method of reference community identification is difficult to apply to ecological restoration of fertilized soils. However, if habitat degradation is limited to mechanical soil disturbance, many soil variables typically driving plant species composition remain unchanged. In our approach, we avoided the use of the soil parameters cited above (total and mineral nitrogen, organic matter) that are known to be influenced by mechanical soil disturbance. Thus, we are convinced that our selected abiotic factors are appropriate for the search of best matching reference sites. Such data collected in situ (contemporary data) may be complemented by historical data (wildfire records, land use changes) that may still affect plant species composition (Asbjornsen et al. 2005; Urgenson et al. 2018). Our method is applicable to ecological restoration beyond grasslands if the specific environmental factors structuring the plant communities are correctly identified. For example, in ecological restoration of lagoon ecosystems corresponding to ancient salt marshes (EU habitat code 1150), environmental factors structuring plant communities are water level, duration of flooding and degree of salinity that may also be used to identify reference communities (Bouzillé 2007). In restoration practice, adjacent sites of very similar environmental conditions are not always available. Either the degradation includes the whole habitat with completely different conditions outside the degraded zone (e.g. degraded grasslands within woodlands), adjacent sites are not accessible (or not available as source sites for seed transfer) or abiotic conditions change at very small scales. In such cases, our approach allows the identification of

most common degradation of European grasslands, increases soil nutrient content, in particular

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geographically more distant reference or source sites that match best with environmental conditions of restoration sites. In this case, the selection of multiple potential references is therefore necessary to select the one(s) that will be closest to the restored sites in terms of environmental variables driving plant community composition. The concept of multiple references is a helpful tool in restoration practice allowing a more flexible choice depending on availability (identification of source sites) or on different priorities for environmental factor match. Additionally, even if the restoration sites are close, the best potential reference sites are not necessarily the same, depending on the environmental factors that can vary on a relatively small scale. Finally, in grassland restoration practice, the identification of multiple references allows to combine different source sites if non-degraded sites do not comprise the entire species pool (area not sufficient, environmental conditions do not fully correspond). Although not directly tested in our proof-of-concept, the method also allows the integration of land management variation resulting in different quasi-stable states of plant succession.

To conclude, our approach to use the close relationships between environmental conditions and plant community composition is a straightforward method to identify reference communities when environmental structuring factors are not affected by degradation. It can be easily applied to restoration practice but requires a good knowledge of plant ecology, in particular on plant-environment interactions, environmental filters and local species pools (Lortie et al. 2004; Cristofoli & Mahy 2010). A better understanding of plant-environment interactions and of potential effects of degradations on physical and chemical soil conditions would be required to improve the method.

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LITERATURE CITED

Alard D, Poudevigne I (2002) Biodiversity in changing landscapes: from species or patch assemblages to system organisation. In: Leuven RSEW, Poudevigne I, Teeuw RM (eds), Application of Geographic Information Systems and Remote Sensing in River Studies, R.S.E.W. Leuven, I. Poudevigne, R.M. Teeuw. Backhuys Publishers, Leiden, The Netherlands, pp 9–24 Aronson J, Clewell A, Moreno-Mateos D (2016) Ecological restoration and ecological engineering: Complementary or indivisible? Ecological Engineering 91:392–395 Aronson J, Floret C, Floc'h EL, Ovalle C, Pontanier R (1993) Restoration and Rehabilitation of Degraded Ecosystems in Arid and Semi-Arid Lands. I. A View from the South. Restoration Ecology 1:8–17 Aronson J, Floret C, Le Floc'h E, Ovalle C, Pontanier R (1995) Restauration et réhabilitation des écosystèmes dégradés en zones arides et semi-arides : le vocabulaire et les concepts. In: L'homme peut-il refaire ce qu'il a défait ? J. Libbey Eurotext, Montrouge, pp 11–29

409	Asbjornsen H, Brudvig LA, Mabry CM, Evans CW, Karnitz HM (2005) Defining Reference
410	Information for Restoring Ecologically Rare Tallgrass Oak Savannas in the Midwestern
411	United States. j for 103:345–350
412	Baasch A, Engst K, Schmiede R, May K, Tischew S (2016) Enhancing success in grassland
413	restoration by adding regionally propagated target species. Ecological Engineering
414	94:583–591
415	Benayas JMR, Newton AC, Diaz A, Bullock JM (2009) Enhancement of Biodiversity and
416	Ecosystem Services by Ecological Restoration: A Meta-Analysis. Science 325:1121-
417	1124.
418	Bischoff A (2002) Dispersal and establishment of floodplain grassland species as limiting
419	factors in restoration. Biological Conservation 104:25–33
420	Bischoff A, Warthemann G, Klotz S (2009) Succession of floodplain grasslands following
421	reduction in land use intensity: the importance of environmental conditions,
422	management and dispersal. Journal of Applied Ecology 46:241-249
423	Box EO (1981) Macroclimate and plant forms: an introduction to predictive modelling in
424	phytogeography. Kluwer, The Hague, NL
425	Bouzillé JB (2007) Gestion des habitats naturels et biodiversité. Concept, méthodes et
426	démarches. Lavoisier, Paris, France 331
427	Cerozi B da S, Fitzsimmons K (2016) The effect of pH on phosphorus availability and
428	speciation in an aquaponics nutrient solution. Bioresource Technology 219:778-781
429	Ciesielski H, Sterckeman T (1997) A comparison between three methods for the determination
430	of cation exchange capacity and exchangeable cations in soils. Agronomie 17:9–15

431	Clewell AF, Aronson J (2013) Ecological Restoration, Second Edition: Principles, Values, and
432	Structure of an Emerging Profession. Island Press
433	Cortina J, Maestre FT, Vallejo R, Baeza MJ, Valdecantos A, Perez-Devesa M (2006)
434	Ecosystem structure, function, and restoration success: Are they related? Journal for
435	Nature Conservation 14:152–160
436	Cristofoli S, Mahy G (2010) Restauration écologique: contexte, contraintes et indicateurs de
437	suivi. Biotechnologie, Agronomie, Société et Environnement 14:203-211
438	Dolan MS, Clapp CE, Allmaras RR, Baker JM, Molina JAE (2006) Soil organic carbon and
439	nitrogen in a Minnesota soil as related to tillage, residue and nitrogen management. Soil
440	and Tillage Research 89:221–231
441	Du Z, Ren T, Hu C (2010) Tillage and Residue Removal Effects on Soil Carbon and Nitrogen
442	Storage in the North China Plain. Soil Science Society of America Journal 74:196–202
443	Erskine PD, Bartolo R, McKenna P, Humphrey C (2019) Using reference sites to guide
444	ecological engineering and restoration of an internationally significant uranium mine in
445	the Northern Territory, Australia. Ecological Engineering 129:61–70
446	Fukami T, Bezemer M, Mortimer S, Vander Putten, WH (2005) Species divergence and trait
447	convergence in experimental plant communities. Ecology Letters, 8:1283-1290.
448	Giardina CP, Litton CM, Thaxton JM, Cordell S, Hadway LJ, Sandquist DR (2007) Science
449	Driven Restoration: A Candle in a Demon Haunted World—Response to Cabin (2007).
450	Restoration Ecology 15:171–176

451	Halle S, Fattorini M (2004) Advances in restoration ecology: insights from aquatic and
452	terrestrial ecosystems. In: Temperton VM et al. Assembly rules and Restoration
453	Ecology., Island Press. Whashington, pp 10–33
454	Härdtle W, Redecker B, Assmann T, Meyer H (2006) Vegetation responses to environmental
455	conditions in floodplain grasslands: Prerequisites for preserving plant species diversity.
456	Basic and Applied Ecology 7:280–288
457	Hobbs RJ, Norton DA (1996) Towards a Conceptual Framework for Restoration Ecology.
458	Restoration Ecology 4:93–110
459	Hölzel N, Otte A (2003) Restoration of a species-rich flood meadow by topsoil removal and
460	diaspore transfer with plant material. Applied Vegetation Science 6:131-140
461	Isselstein J, Jeangros B, Pavlu V (2005) Agronomic aspects of biodiversity targeted
462	management of temperate grasslands in Europe – A review. Agronomy Research 3:139–
463	151
464	Kiehl K, Kirmer A, Donath TW, Rasran L, Hölzel N (2010) Species introduction in restoration
465	projects - Evaluation of different techniques for the establishment of semi-natural
466	grasslands in Central and Northwestern Europe. Basic and Applied Ecology 11:285-
467	299
468	Klimek S, Richter gen. Kemmermann A, Hofmann M, Isselstein J (2007) Plant species richness
469	and composition in managed grasslands: The relative importance of field management
470	and environmental factors. Biological Conservation 134:559–570
471	Le Floch E, Aronson J (1995) Écologie de la restauration. Définition de quelques concepts de
472	base. Natures Sciences Sociétés, Hors série. 3:s29-s35

4 <i>7</i> 3	species data. Oecologia 129:271–280
475	Li F-R, Liu L-L, Liu J-L, Yang K (2019) Abiotic and biotic controls on dynamics of labile
476	phosphorus fractions in calcareous soils under agricultural cultivation. Science of The
477	Total Environment 681:163–174
478	Lortie CJ, Brooker RW, Choler P, Kikvidze Z, Michalet R, Pugnaire FI, Callaway RM (2004)
479	Rethinking plant community theory. Oikos 107:433–438
480	McCune B, Grace JB (2002) Analysis of ecological communities, MjM Software Design,
481	Gleneden Beach, Oregon.
482	McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat
483	load. Journal of Vegetation Science 13:603-606
484	McDonald T, Gann GD, Jonson J, Dixon KW (2016) International standarts for the practice of
485	ecological restoration - includind principles and key concepts (first edition), Society for
486	Ecological Restoration (SER), Washington, D.C
487	McManamay RA, Smith JG, Jett RT, Mathews TJ, Peterson MJ (2018) Identifying non-
488	reference sites to guide stream restoration and long-term monitoring. Science of The
489	Total Environment 621:1208–1223
490	Oksanen J, Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn Dol et al. (2019) vegan:
491	Community Ecology Package. R package version 2.5-4
492	Olsen SR (1954) Estimation of Available Phosphorus in Soils by Extraction with Sodium
493	Bicarbonate. U.S. Department of Agriculture

494	Palmer MA, Ambrose RF, Poff NL (1997) Ecological Theory and Community Restoration
495	Ecology. Restor Ecology 5:291–300
496	Prach K, Tichý L, Lencová K, Adámek M, Koutecký T, Sádlo J et al. (2016) Does succession
497	run towards potential natural vegetation? An analysis across seres. Journal of
498	Vegetation Science 27:515–523
499	Pykälä J, Luoto M, Heikkinen RK, Kontula T (2005) Plant species richness and persistence of
500	rare plants in abandoned semi-natural grasslands in northern Europe. Basic and Applied
501	Ecology 6:25–33
502	R Core Team (2019) R: A language and environment for statistical computing. R Foundation
503	for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/
504	Ruiz-Jaen MC, Aide TM (2005) Restoration Success: How Is It Being Measured? Restoration
505	Ecology 569–577
506	Sebastiá M-T (2004) Role of topography and soils in grassland structuring at the landscape and
507	community scales. Basic and Applied Ecology 5:331–346
508	SER Primer: Society for Ecological Restoration International (2004) Science & Policy Working
509	Group. The SER International Primer on Ecological Restoration. www.ser.org &
510	Tucson: Society for Ecological Restoration International.
511	Scotton M, Kirmer A, Krautzer B (2011) Practical handbook for seed harvest and ecological
512	restoration of species-rich grasslands. Practical handbook for seed harvest and
513	ecological restoration of species-rich grasslands

514	Sluis WJ, Bowles M, Jones M (2018) Multiscale metrics differentiate among tallgrass prairie
515	restorations and remnant ecosystems along a restorative continuum. Restoration
516	Ecology 26:466–475
517	Srinivasan MP, Bhatia S, Shenoy K (2005) Vegetation-environment relationships in a South
518	Asian tropical montane grassland ecosystem: restoration implications. Tropical Ecology
519	56:201–221
520	Suganuma MS, Durigan G (2015) Indicators of restoration success in riparian tropical forests
521	using multiple reference ecosystems. Restoration Ecology 23:238–251
522	Tallowin, JRB, Kirkham FW, Smith REN, Mount-ford JO (1998) Residual effects of
523	phosphorous fertilisation on the restoration of floristic diversity to wet hay meadows.
524	In: Joyce CB and Wade PM (eds) European Lowland Wet Grasslands: Biodiversity,
525	Management and Restoration, John Wiley & Sons, Ltd., Chichester, United Kingdom,
526	pp. 249-263
527	Thomas GW (1982) Exchangeable Cations. Methods of Soil Analysis Part 2 Chemical and
528	Microbiological Properties agronomymonogra:159–165
529	Urgenson LS, Nelson CR, Haugo RD, Halpern CB, Bakker JD, Ryan CM et al. (2018) Social
530	perspectives on the use of reference conditions in restoration of fire-adapted forest
531	landscapes. Restoration Ecology 26:987–996
532	Vander Mijnsbrugge K, Bischoff A, Smith B (2010) A question of origin: Where and how to
533	collect seed for ecological restoration. Basic and Applied Ecology 11:300-311

534	Wortley L, Hero J-M, Howes M (2013) Evaluating Ecological Restoration Success: A Review
535	of the Literature: Trends and Gaps in Empirical Evaluations. Restoration Ecology
536	21:537–543
537	Young TP, Petersen D A, Clary JJ (2005) The ecology of restoration: historical links, emerging
538	issues and unexplored realms. Ecology Letters 8:662–673
539	Young TP, Chase JM, Huddleston RT (2001) Community Succession and Assembly
540	Comparing, Contrasting and Combining Paradigms in the Context of Ecological
541	Restoration. Ecological Rest 19:5–18
542	Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common
543	statistical problems. Methods in Ecology and Evolution 1:3–14
544	
545	
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Table 1. Similarities between restoration sites (1R, 2R, 3R, 11R, 20R) and the non-degraded sites (from site 4 to 24, without R) of the study zone (similarity decreasing from left to right) using the Euclidean distance for environmental variables shown in Fig. 3. Here the colors show examples for chosing only one reference for (a) one site (example of restoration site 2R: \triangle); (b) 2 sites (example of 1R and 3R: \bigcirc); (c) all the restoration sites (1R, 2R, 3R, 11R and 20R: \bigcirc).

Restoration sites	Hig	Higher similartity —							eren	ce sit	es		→ Lower similarity					
1R	16	22	9	23	15	19	4	17	18	13	6	5	8	16	10	7	12	14
2R	6	4	5	15	9	16	16	8	18	7	19	13	23	10	22	12	17	14
3R	16	18	15	6	19	9	4	22	8	23	5	13	16	17	7	10	12	14
11R	12	10	16	13	9	14	7	5	8	15	17	19	18	22	4	6	16	23
20R	9	17	14	19	10	22	16	12	7	13	16	18	4	15	8	6	5	23

Fig. 1. The four major steps of the proposed method to select references. ① Delimit an extend study area around restoration sites; ② Identify environmental factors structuring plant communities (data collection and driver analysis); ③ Evaluate environmental distances between restoration and potential reference sites (dissimilarity coefficient); ④ Select the most similar references to restoration sites (dissimilarity coefficient).

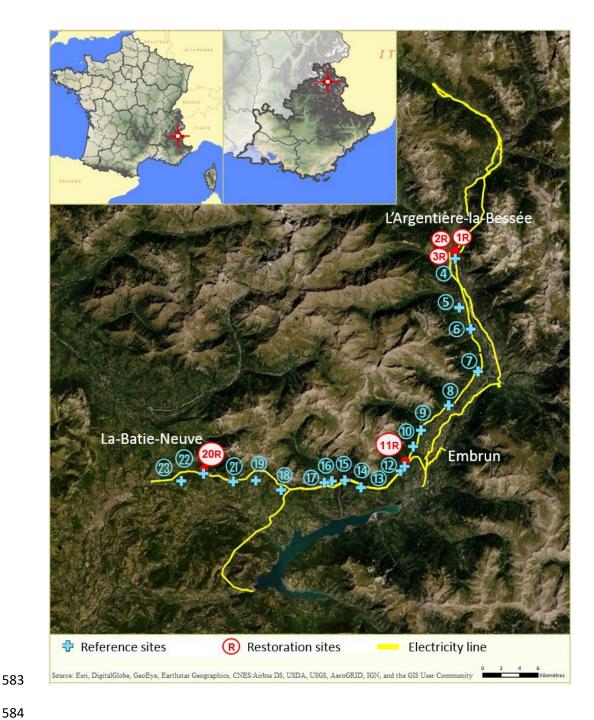


Fig. 2. Location of the study area with restoration sites (1R, 2R, 3R, 11R and 20R, in red) and reference sites (numbered from north to south, without R, in blue) along the construction of a new electricity line.

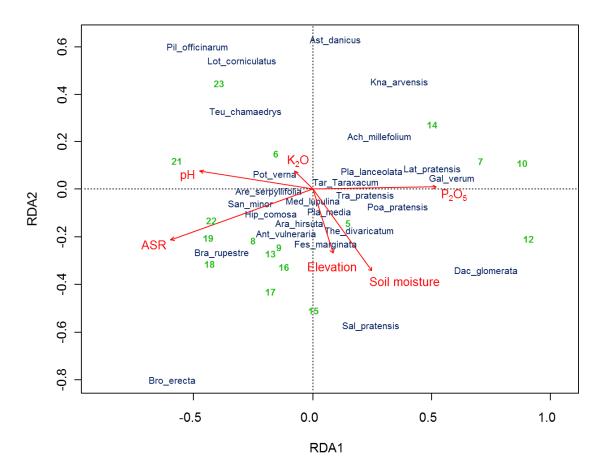


Fig. 3. RDA biplot using Hellinger-transformed plant species cover (species names in blue) and reference sites (green) constrained by environmental variables (red arrows). Environmental variables: ASR = Annual Solar Radiation; P_2O_5 = plant available phosphorous; soil moisture; soil pH; elevation and K_2O = plant available potassium. Full species names: Table S3.

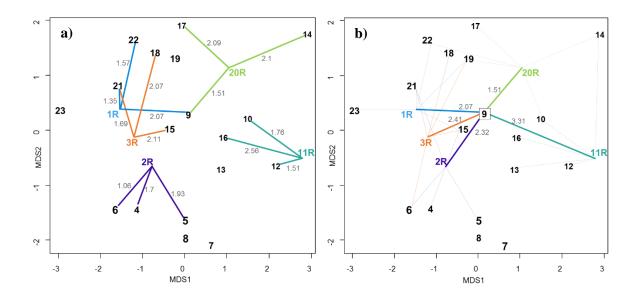


Fig. 4. NMDS based on environmental variables showing a) the three most similar non-degraded sites (without R) for each restoration site (with R) and b) the non-degraded site that present the lowest average environmental distance with all the restoration sites. Different restoration sites are represented by different colors. The grey numbers represent the environmental distance (dissimilarity coefficient). See Table 1 for more details.